SELECTIVE PREDATION ON SCANSORIAL AND ARBOREAL MAMMALS BY RUFOUS-LEGGED OWLS (*STRIX RUFIPES*) IN SOUTHERN CHILEAN RAINFOREST

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ABSTRACT.—We estimated the annual mammalian diet of Rufous-legged Owls (*Strix rufipes*) in three temperate rainforest sites in southern Chile (Anticura, Rupanco and San Martín), and mammal abundance at San Martín and Anticura. Diets were estimated by analysis of 894 pellets collected from 1988–95. In all sites, arboreal (arboreal mouse, *Irenomys tarsalis* and colocolo opossum, *Dromiciops australis*) and scansorial (long-tailed mouse, *Oryzomys longicaudatus*) mammals occurred significantly more frequently than those mammals with cursorial habits, such as the olivaceous field mouse (*Akodon olivaceus*) and long-haired field mouse (*A. longipilis*). Although the body size and abundance of the olivaceous field mouse were similar to those of the long-tailed mouse, the former species was seldom taken by Rufous-legged Owls, likely because it was associated with vegetational features that offer overhead protection.

KEY WORDS: Strix rufipes; *Rufous-legged Owl; prey selection; Patagonian Wood Owl; Chile; temperate forest.*

Depradación selectiva sobre mamíferos escansoriales y arborícolas por concones (*Strix rufipes*) en la pluviselva del sur de Chile

RESUMEN.—Estimamos la dieta anual del búho de bosque o concón (*Strix rufipes*) en tres localidades de pluviselva templada (Anticura, Rupanco y San Martín) y la relacionamos con la abundancia anual de micromamíferos presentes en San Martín y Anticura. La dieta se determinó mediante el análisis de 894 egagrópilas colectadas entre 1988–95. En los tres sitios, los micromamíferos de hábitos arborícolas (*Irenomys tarsalis* y *Dromiciops australis*) y escansoriales (*Oryzomys longicaudatus*) fueron significativamente más depredados que los de hábitos cursoriales tales como *Akodon olivaceus* y *A. longipilis*. A pesar que *A. olivaceus* exhibió abundancia en terreno y tamaño corporal similares a los de *O. longicaudatus*, casi no fue depredado por los búhos. Esto puede atribuirse a su asociación con variables vegetacionales que le ofrecerían protección desde un plano vertical.

[Traducción de autores]

The Rufous-legged Owl or Patagonian Wood Owl (*Strix rufipes*) is one of the least known nocturnal raptors of South America, inhabiting the temperate rainforest region shared by Chile and Argentina (Jaksić 1997). What information there is about this species is either anecdotal (Housse 1945, Johnson 1967) or consists of brief accounts on taxonomy and distribution (e.g., Humphrey et al. 1970, Vuilleumier 1985, Jaksić and Feinsinger 1991).

From a conservation viewpoint, Glade (1988) listed this species as inadequately known. While the Rufous-legged Owl is relatively common it is con-sidered to be declining in southern Chile because of decreasing habitat brought about by logging (Jaksić and Jiménez 1986). This was confirmed when Martínez and Jaksić (1996) reported the first quantitative information on the relative abundance of Rufous-legged Owls in forest remnants of southern Chile, and described forest stands used by these owls.

The first quantitative report on the diet of the Rufous-legged Owl was based on an analysis of 161 pellets (Martínez 1993). Although the study concluded that Rufous-legged Owls are generalist feeders, the most frequent vertebrate prey were arbo-

real and scansorial small mammals. Cursorial species, despite their similar or higher diversity (Meserve and Jaksić 1991), were poorly represented. Here, we report additional data on the diet of Rufous-legged Owls that inhabit three rainforest stands in southern Chile and test the assumed selective predation noted by Martínez (1993).

STUDY AREAS AND METHODS

We studied Rufous-legged Owls in three sites in the Valdivian Rainforest region of southern Chile (sensu Veblen et al. 1983). The first site was the San Martín Experimental Forest (39°38'S, 73°11'W; 20 m elevation) in the coastal ranges near the city of Valdivia. This 150-ha site was covered by a second-growth multistoried forest remnant dominated by Aextoxicon punctatum and Podocarpus saligna with substantial Gevuina avellana and some scattered old individuals of emergent Nothofagus dombeyi. The understory was sparse, and the soil was covered with a thick layer of mosses and litter.

The second site was a 180-ha second-growth forest near Lake Rupanco (40°45'S, 72°38'W; 150 m elevation) that consisted of an almost pure stand of A. punctatum with some Laurelia sempervirens, G. avellana and old N. dombeyi trees.

The third site, Anticura (40°40'S, 72°10'W; 600 m elevation), was an extensive preAndean forest located in Puyehue National Park, near the city of Osorno. It was a multistoried old-growth stand with emergent trees (N. dombeyi) 35–40 m in height; also present were L. phillipiana, Eucryphia cordifolia and shade-tolerant trees such as Weinmania trichosperma and A. punctatum. Shrubs were scarce and the understory was comprised of saplings of shade-tolerant trees, ferns, a few bromeliads and both bamboo (Chusquea spp.) and Ribes magellanicum clumps. The ground was covered by mosses (Sphagnum sp.), and in damp areas ferns reached tree-like sizes.

Owl pairs were resident in all three sites year-round and their pellets were collected under roosting trees. In San Martín, we collected 72 pellets from April 1988 (early autumn)–February 1990 (late summer). In Rupanco, we collected 347 pellets from February 1993–September 1995 (early spring) and, in Anticura, we collected 475 pellets from September 1994–October 1995 (spring). We identified and quantified most vertebrates in the pellets on the basis of skulls and dentary pairs, whichever gave the highest count. For other remains, such as hair, we used reference collections and quantified these prey assuming the smallest possible number of individuals (e.g., presence of hair of a given species was deemed as representing only one individual). We estimated the biomass contribution of each prey type in the diet by multiplying the number of individuals in the pellet by the mean body mass of that prey item. We assumed that masses of unidentified prey were similar to the average mass of the most closely related identified taxa. We did not consider nonmammalian prey items, because their contribution to the biomass consumed was minimal in all sites (<10%).

In San Martín, small mammal abundance was evaluated from 1988–89 in a 12 × 12 grid of medium-sized Sherman live traps. Trapping stations were set 12 m apart and

equipped with one trap for a total of 144 traps covering an area measuring 132 × 132 m (1.7 ha). Each census lasted six consecutive nights every month for a full year. The mean annual abundance (recaptures were not considered) of each small mammal species trapped was used to estimate the expected frequency of prey consumption by Rufous-legged Owls (e.g., proportion of mammal species i in the field with regard to the abundance of all species trapped). The actual prey identified in the diet constituted the observed frequency. For Anticura, we used data reported by Rau et al. (1995), who assessed the abundance of ground-dwelling small mammals with two trap lines 2 m apart with 30 stations set at 12-m intervals and equipped with one medium-sized Sherman trap per station for a total of 60 traps in an area measuring 348 × 4 m (0.14 ha). Rau et al. (1995) simultaneously estimated the abundance of tree-dwelling small mammals with 60 hair-sampling tubes nailed to trees along the trap lines. An empirical estimate of abundance was obtained by pooling these data, given that the trapping effort was the same for ground- and tree-dwelling small mammals.

A Chi-square test was performed to test the goodness-of-fit of the frequency distributions of prey in the diet and in the field (Zar 1984). Nonsignificant values were interpreted as if Rufous-legged Owls used prey in proportion to their field abundance, whereas significant deviations suggested that Rufous-legged Owls "preferred" or "avoided" some small mammal species, thus appearing to select prey.

Because with the Chi-square test it is not possible to determine which prey species was individually avoided or preferred, we constructed confidence intervals for each prey using the Bonferroni adjustment (Neu et al. 1974, Byers et al. 1984):

$$p_i - z_{a/2k}\sqrt{p_i(1 - p_i)}/n \le p_i \le p_i + z_{a/2k}\sqrt{p_i(1 - p_i)}/n,$$

where p_i is the proportion of consumption of prey species i, k is the number of prey species, n is the total number of prey and $z_{a/2k}$ is the upper standard normal variate corresponding to a probability tail area of a/2k. The 2k denominator under a is used because multiple confidence intervals were computed simultaneously. If the confidence interval included the expected proportion of consumption (p_{io}), then we did not reject the hypothesis that prey species were preferred or avoided. If the expected proportion of consumption was not included in the interval, we concluded that observed and expected consumption differed significantly. Statistical significance was set at $P \le 0.05$ for all tests unless otherwise stated.

RESULTS

In the three sites, both by number and biomass, the scansorial long-tailed mouse (Oryzomys longicaudatus) was the staple prey for Rufous-legged Owls (Table 1). Although the biomass contribution made by the arboreal mouse (Irenomys tarsalis) was lower, it was consistently eaten at all sites. This was also true of the scansorial black rat (Rattus rattus). Only in San Martín was the consumption of the arboreal colocolo opossum (Dromiciops australis) important.

Table 1. Vertebrate prey of Rufous-legged Owls (*Strix rufipes*) in Anticura, Rupanco, and San Martín (Chile). Below each prey species are denoted temporal (N = nocturnal, D = diurnal) and spatial (F = fossorial, C = cursorial, S = scansorial, A = arboreal) activities, and mass[a] in grams. B% is percent of prey by biomass and N is frequency of prey by number.

VERTEBRATE PREY	ANTICURA		RUPANCO		SAN MARTÍN	
	B%	(N)	B%	(N)	B%	(N)
Akodon longipilis (D-N; C; 41)	29.7	(155)	0.8	(2)	0.0	(0)
Akodon olivaceus (N; C; 23)	0.8	(7)	1.7	(8)	1.4	(1)
Auliscomys micropus (N; C; 58)	1.6	(6)	1.1	(2)	3.4	(1)
Geoxus valdivianus (D-N; F; 25)	2.1	(18)	0.2	(1)	0.0	(0)
Irenomys tarsalis (N; A; 42)	10.0	(51)	6.8	(17)	5.0	(2)
Oryzomys longicaudatus (N; S; 26)	50.0	(411)	56.2	(228)	35.7	(23)
Phyllotis darwini (N; C; 66)	0.0	(0)	1.2	(2)	0.0	(0)
Rattus rattus (N; S; 40[b])	0.4	(2)	4.2	(11)	12.0	(5)
Unidentified rodents[c]	5.3	(31)	25.5	(67)	11.2	(5)
Dromiciops australis (N; A; 34)	0.0	(0)	2.3	(7)	30.4	(15)
Rhyncholestes raphanurus (N; S; 29)	0.1	(1)	0.0	(0)	0.0	(0)
Unidentified bat (A; 15)	0.0	(0)	0.0	(0)	0.9	(1)
Total prey items	682		345		53	
Total biomass (g)	21 379		10 546		1677	
Total pellets	475		347		72	

[a] Masses for mammals were obtained from Martínez (1993) and references therein, and from D.R. Martínez (unpubl. data) for the remaining taxa.

[b] Juveniles.

[c] Mean masses of unidentified prey for each locality: Anticura: 37 g; Rupanco: 40 g; San Martín: 38 g.

In general, the most frequent prey were arboreal and/or scansorial small mammals. In Anticura, they were 60% of the biomass, whereas in Rupanco they reached 70% and >80% in San Martín. Only in Anticura was the cursorial long-haired field mouse (*Akodon longipilis*) heavily preyed upon. Together, the remaining cursorial rodents, olivaceous field mouse (*A. olivaceus*), austral greater mouse (*Auliscomys micropus*), and Darwin's leaf-eared mouse (*Phyllotis darwini*), contributed <5% of the biomass consumed in all sites.

In San Martín, 837 individuals belonging to five species of small mammals were caught during 20 736 trap-nights, whereas in Anticura 59 individuals of six species were caught during 358 trap-nights and detected during 8095 tube-nights conducted simultaneously (Table 2). While the traps in San Martín captured five small-mammal species, Rufous-legged Owls captured six species (Tables 1 and 2). In Anticura, six species were captured by Rau et al. (1995), but Rufous-legged Owls caught eight species (Tables 1 and 2).

At both sites, the frequency distributions of small mammal species observed in Rufous-legged Owl pellets (Table 1), compared to those estimated in the field through trapping (expected values, Table 2), were significantly different. In San Martín, the olivaceous field mouse was "avoided," whereas the long-tailed mouse and the pooled species (due to restrictions of the Chi-square test) were "pre-

Table 2. Proportion of captures (p$_i$) calculated from live trapping (recaptures not included) of small mammals present in San Martín. Data for Anticura were obtained from Rau et al. (1995).

SMALL MAMMALS	ANTICURA (p$_i$)	SAN MARTÍN (p$_i$)
Akodon longipilis	0.571	0.120
Auliscomys micropus	0.000	0.007
Akodon olivaceus	0.368	0.461
Geoxus valdivianus	0.003	0.000
Irenomys tarsalis	0.000	0.007
Oryzomys longicaudatus	0.049	0.405
Dromiciops australis	0.003	0.000
Rhyncholestes raphanurus	0.006	0.000
Total individuals	59	837
Total trap-nights	8453	20 736

ferred" (Table 3). In Anticura, the long-tailed mouse accounted for more than 80% of the Chi-square value, suggesting that, as in San Martín, it was the preferred prey species.

In Anticura, the expected proportions of use of three prey species exceeded the Bonferroni confidence intervals (Table 4). The cursorial long-haired and olivaceous field mice were consumed less and the scansorial long-tailed mouse was consumed more than expected. In San Martín, as in Anticura, the olivaceous field mouse was consumed less and the long-tailed mouse more than expected (Table 4). Overall, arboreal and scansorial small

mammals constituted the core of the Rufous-legged Owl diet, whereas cursorial small mammals, despite their similar field abundance (Martínez 1993), were poorly represented in the diet.

DISCUSSION

In all three sites, the frequency of the scansorial long-tailed mouse in the diet of Rufous-legged Owls was high. The low consumption of the cursorial olivaceous field mouse was noteworthy because this species was numerically codominant with the long-tailed mouse, at least in San Martín (Murúa and González 1986). Considering their similar body masses (23 g for olivaceous field mouse and 26 g for the long-tailed mouse, this trait may not explain avoidance or preference.

Alternatively, different escape tactics or detectability of these two species may be involved. Murúa and González (1982) attributed the different microhabitat selection of olivaceous field mice and long-tailed mice to predation pressure. The former species is associated with vegetational variables that provide greater cover from above implying avoidance of aerial predators. The latter species is associated with dense areas with understory that offer protection from a horizontal viewing implying avoidance of terrestrial predators.

In addition, different antipredatory behaviors have been documented for those two rodents, as well as for other rodent species consumed by Rufous-legged Owls. Mann (1978) reported that, because of its long hind legs, the long-tailed mouse

Table 3. Absolute frequencies of observed and expected consumption of small mammals by Rufous-legged Owls in Anticura and San Martín (Chile).

| SMALL MAMMALS | ANTICURA | | SAN MARTÍN | |
	OBSERVED	EXPECTED	OBSERVED	EXPECTED
Akodon longipilis	155	372.0	1	21.6
Akodon olivaceus	7	239.0	0	5.6[a]
Auliscomys micropus	6	0.0[a]	1	0.3[a]
Geoxus valdivianus	18	2.0[a]	—	—
Irenomys tarsalis	51	0.0[a]	2	0.3[a]
Oryzomys longicaudatus	411	32.0	23	19.1
Rattus rattus	2	0.0[a]	5	0.0[a]
Dromiciops australis	0	2.0[a]	15	0.0[a]
Rhyncholestes raphanurus	1	4.0[a]	—	—
Pooled species[a]	78	8.0	23	6.2
Total pellets	475		72	
Chi-square (df)	452.9 (3)	$P < 0.001$	65.69 (2)	$P < 0.001$

[a] Pooled because expected values were <5.0.

Table 4. Bonferroni confidence intervals for the proportion of utilization of prey types, p_i, by Rufous-legged Owls in Anticura and San Martín (Chile). An asterisk indicates a difference at the 0.05 level of significance. (+) eaten more than expected by chance; (−) eaten less than expected by chance.

SMALL MAMMALS	EXPECTED PROPORTION OF USE (p_{io})	OBSERVED PROPORTION OF USE (p_i)	BONFERRONI'S INTERVALS FOR p_i
Anticura			
Akodon longipilis	0.571	0.297	$0.248 \leq p_i \leq 0.346$ (−)*
Akodon olivaceus	0.368	0.008	$0.007 \leq p_2 \leq 0.009$ (−)*
Oryzomys longicaudatus	0.049	0.500	$0.447 \leq p_3 \leq 0.553$ (+)*
San Martín			
Akodon olivaceus	0.461	0.040	$0.000 \leq p_1 \leq 0.127$ (−)*
Auliscomys micropus	0.007	0.040	$0.000 \leq p_2 \leq 0.127$
Oryzomys longicaudatus	0.405	0.850	$0.690 \leq p_3 \leq 1.000$ (+)*
Irenomys tarsalis	0.007	0.070	$0.000 \leq p_4 \leq 0.184$

was able to escape predators by jumping away into open fields and Glanz (1982) reported that it climbs up shrubs as an escape response. In contrast, the short-legged rodents (*Phyllotis* spp. and *Akodon* spp.), make only short quadrupedal runs toward the nearest shelter (Mann 1978) or exhibit "freezing" behavior when presented overhead raptor silhouettes in laboratory experiments (Simonetti 1986).

The microhabitat type used by these rodent species and their antipredatory behaviors, coupled with the hunting mode of Rufous-legged Owls could lead to differential predation pressures, regardless of the local abundance of these prey. Rufous-legged Owls are sit-and-wait predators closely associated to old-growth stands (Martínez and Jaksić 1996). Hence, prey that venture on branches or climb on trees, or move from one spot to another, leaping on the ground, may be more easily detected by this owl than sympatric cursorial rodents that commonly move along runways.

Similar habitat use and antipredatory behavior could also explain the high incidence of long-tailed mice in a dietary study of other owls inhabiting central Chile. As shown by Jaksić et al. (1981), both Barn Owls (*Tyto alba*) and Great Horned Owls (*Bubo virginianus*) consumed 70% more long-tailed than olivaceous field mice, whereas the incidence of long-tailed mouse in the diet of terrestrial predators such as foxes was consistently low (Iriarte et al. 1989). Specifically for San Martín, Martínez et al. (1993) reported that gray foxes (*Pseudalopex griseus*) preyed preferentially on olivaceous field mice and long-tailed mice.

Other prey, such as the arboreal mouse, colocolo opossum, bats, birds (Furnariidae) and insects (cockroaches, tree crickets and beetles), are strongly associated with temperate rainforests. By eating these organisms found in the forest canopy, Rufous-legged Owls may exploit resources not utilized by other predators, thus reducing the potential for competition. Although other owl species inhabit southern Chile, their smaller sizes or different habitats may reduce food competition. Thus, the Austral Pygmy Owl (*Glaucidium nanum*) is a smaller forest species that specializes on birds, and its preferred hunting grounds are forest edges and parklands. The sympatric Burrowing (*Speotyto cunicularia*), Barn and Short-eared (*Asio flammeus*) Owls nest and hunt mostly in open areas (D.R. Martínez, unpubl. data).

Because scansorial and arboreal small mammals are closely associated with forest landscapes, the accelerated loss of southern Chilean temperate rainforests is reducing the survival odds for both Rufous-legged Owls and their prey. Even in the best possible scenario where there is an increase of suitable small mammals in cutover areas, the stereotyped hunting mode, a reduction of roosting and nesting sites and the increased presence of potential competitors (open-field owls) may eventually lead to the extinction of this forest-adapted owl species.

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